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THEORETICAL ARTICLE

The Evolution of Human Female Sexual Orientation

Austin John Jeffery[1] · Todd K. Shackelford[1] · Virgil Zeigler-Hill[1] · Jennifer Vonk[1] · Melissa McDonald[1]

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Abstract
Female sexual orientation has received less theoretical and empirical attention than male sexual orientation and few reviews are devoted to female sexual orientation. Moreover, research investigating female sexual orientation often underappreciates insights afforded by evolutionary theory. This review begins with an overview of the literature on female sexual identification, sexual perception, sexual fluidity, sexual expression, and the biology of female sexual orientation. Female same-sex sexual behaviors in the non-human apes are then described, providing a comparative context for the following discussion of hypotheses for the evolution of human female same-sex sexual attractions and behaviors. These hypotheses are organized as byproduct hypotheses or adaptation hypotheses and we include discussions of dysfunction, heterosis, sexual antagonism, epigenetics, weak selection, self-domestication, sexual frustration, mate attraction, alloparenting, polygyny, and other topics. We conclude by highlighting the challenges posed by evolutionary studies of human psychology.

Keywords Evolution · Female homosexuality · Female sexuality · Sexual orientation

Same-sex sexual attractions and behaviors, to the extent that they are exclusive and attributable to genetic influence, are often presented as deleterious because they may subtract from lifetime reproductive success (Gates 2013). Yet, same-sex sexual attractions and behaviors are expressed by a large minority of humans. This apparent paradox has inspired a substantial and growing literature on the mechanisms and evolutionary factors that account for variations in human sexual orientation. However, much of the literature focuses on male sexual orientation and fails to illustrate the factors that make female sexual orientation uniquely interesting and challenging. This review begins descriptively, providing an overview of what is known about the expression of female sexual orientation and what can be inferred from theoretical and experimental work. We then explore each of the major hypotheses for the evolution and development of female-female sexual attractions and behaviors. Throughout the review, we make reference to principles and data from evolutionary theory, history, anthropology, and comparative research. Individual human sexual psychology and behavior is perhaps best understood as a product of proximate biological, developmental, and social factors, but understanding universal and sex-differentiated features of human sexual psychology and behavior requires consideration of fundamental evolutionary forces (Gray 2013).

✉ Austin John Jeffery
geffaust@gmail.com

[1] Department of Psychology, Oakland University, Rochester, MI 49309, USA

Introduction to Human Sexual Orientation

In the following discussion, the term *sexual orientation* refers to the pattern of psychological, physiological, and behavioral responses to sexual stimuli. The term *sexual expression* refers to culture-bound manifestations and perceptions of sexual orientation. The terms *homosexual*, *heterosexual*, *bisexual*, and *queer* refer to particular Western sexual expressions, and will be applied only to individuals and samples who identify themselves as such. Between 1 and 3% of American women identify as homosexual, although between 10 and 20% report having experienced same-sex sexual attractions and/or behaviors (Gates 2011; Mercer et al. 2007; Savin-Williams and Ream 2007). Whereas non-heterosexual men are most likely to identify as homosexual, non-heterosexual women are most likely to identify as bisexual or queer (Gates 2011), and heterosexual women are also more likely than heterosexual men to report same-sex sexual attractions (Chivers 2017). Thus, female same-sex sexual attractions and behaviors rarely entail homosexual identification. Additionally, the homosexual identity

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may have little evolutionary relevance (i.e., the shared, identifiable, cultural conception of sexual orientation may be evolutionarily novel). Most self-report measures of sexual orientation present categorical or bipolar response options (Sell 1997), making it difficult to detect continuous and multidimensional features of sexual orientation. Vrangalova and Savin-Williams (2012) argue that the distribution of responses across categories suggests an underlying continuity consisting of two independent dimensions: sexual attraction to males and sexual attraction to females (androphilia and gynephilia, respectively). For men, the case for discrete "kinds" of sexual orientation is stronger (Norris et al. 2015), and these categories (e.g., gay and straight) distinguish men on other features, including sociosexuality and sexual jealousy, but do not distinguish women (Howard and Perilloux 2017). In other words, women demonstrate greater sexual fluidity than men.

Sexual fluidity refers to the diversity of stimuli and contexts that produce a sexual response in an individual (Diamond 2008). This sexual response is broadly defined and can include sexual or romantic attraction, physiological arousal, and/or sexual behavior. Kanazawa (2016) describes sexual fluidity in three domains: the degree of exclusivity in one's sexual response to available stimuli, the degree of change in the stimuli that produces a sexual response across time, and the degree of variance or disagreement between different measures of the sexual response (e.g., a behaviorally heterosexual woman experiencing same-sex sexual fantasies). Thus, individuals with high sexual fluidity experience sexual responses toward a broad and shifting range of stimuli (Chivers 2017; Diamond 2008). Male sexual desire is usually considered category-specific, as it strongly favors one sex (Chivers and Bailey 2005; Lippa 2006; cf. Rosenthal et al. 2011). For men, there is a negative correlation between sexual attraction to one sex and sexual attraction to the other sex, and men of all sexual orientations with higher sex drives have more sex with a single preferred sex (Lippa 2007). This is not true of women, who show a weak positive correlation between attraction to one sex and attraction to the other sex (Lippa 2007).

Eye-tracking studies indicate that men's (but not women's) initial attention to and perception of nude human stimuli is powerfully biased by the apparent sex of the stimuli (Dawson and Chivers 2016). Unconscious, pre-attentional systems orient men toward stimuli of the preferred sex and appraise the stimuli as "sexual," whereas women attend to both preferred and non-preferred stimuli and appraise both as "sexual" (Janssen et al. 2000; Snowden and Gray 2013). Following initial attention to a stimulus, men remain more sex-biased in controlled attention, sexual attraction, and physiological arousal than women (Chivers et al. 2004; Dawson and Chivers 2016). Relative to males, female sexual ambivalence, and inhibitory control may be a product of selection for more prudent mate choice and the avoidance of male sexual aggression (Bjorklund and Kipp 1996). Finally, women report more frequent shifts in sexual attractions than men across their lifetimes, particularly among non-heterosexuals (Diamond 2008; Dickson et al. 2003; Mock and Eibach 2012). Some theorists have suggested that this is the result of greater female sensitivity to normative influences that can affect female sexual orientation (Baumeister 2000), but subsequent research has failed to support this hypothesis (Benuto and Meana 2008).

Human Female Same-Sex Sexual Expression

In the West, the process of "coming out" has been traditionally modeled as a linear, staged process of experiencing same-sex attractions, investigating and verifying those attractions, and finally overcoming fears and doubts in a public declaration of a new identity as a homosexual (the "disclosure imperative"; Coleman 1982; Dank 1971). These views of homosexuality emphasize the effort to discover and embrace one's "true" sexuality. Modern perspectives have identified that female sexuality development is diverse, and notably more diverse than male sexuality development—which much of the traditional theory targets (Diamond 2000; Horowitz and Newcomb 2002; Rust 1993). Diamond and Savin-Williams (2000) found that early same-sex sexual experiences and their timing have less of an impact on sexual orientation than early same-sex sexual attractions (i.e., cognitive and emotional responses to attractions inform identity development) and the diversity of female sexuality development depends on those individual processes. Other important factors include personality characteristics that are associated with the development and expression of heterosexuality, such as risk-taking, independence, and arousability (Bancroft 1989; Udry et al. 1995). One consistent finding is that more psychologically feminine women are more likely to identify as bisexual, and more psychologically masculine women are overwhelmingly more likely to identify as homosexual (Burri et al. 2015; Hiestand and Levitt 2005).

Around the world, the history of and variance in human female-female sexual expression is a challenging topic because, in many cultures, no terminology has been developed to identify female same-sex sexual orientations and (relatedly) because female-female sex has been marginalized by historical perspectives that question or discredit female sexual variance or its importance (Sullivan and Jackson 2001). For example, under Paragraph 175 of the criminal code, homosexual men in Nazi Germany were quantified, questioned, and imprisoned by the tens of thousands, but sex between women was never criminalized, rarely recorded, and only recently have the experiences of the few accused women been documented (Huneke 2017). Cultures differ in their perception and tolerance of same-sex sexual expressions and often enforce

different sexual norms for the sexes, confounding attempts to describe general and sex-specific patterns in sexual orientation. Most of the available research on human sexual orientation has been conducted on so-called WEIRD populations (Western, educated, industrialized, rich, and democratic) and may not be widely generalizable (Heinrich et al. 2010). Globally, same-sex sexual expression in men and women can be organized into three broad categories. "Transgenerational" refers to same-sex relationships between gender-congruent individuals of differing sexual maturity, such that one is an adult and the other is a minor. "Transgendered" refers to same-sex relationships in which one member expresses sex-typical gendered traits and the other expresses opposite-sex-typical gendered traits, such that one member resembles a male and the other resembles a female in interests, dress, and roles, although they share a biological sex (and they may or may not both identify as female). "Egalitarian" refers to same-sex relationships between two gender-congruent adults of similar age, such that both express the sex-typical interests, dress, and roles of their culture (Murray 2000). These typologies exist on a continuum and features of each frequently overlap, but they provide a framework for organizing recurring patterns of sexual expression (for more on sexual expression, see van Anders 2015).

Transgenerational Female Same-Sex Sexual Expression

Although transgenerational same-sex sexual relationships are more often associated with men, several striking examples of female-female transgenerational sexual relationships can be found in ancient cultures. Spartan culture in ancient Greece included an initiation rite in which an adult woman would have intercourse with young girls prior to marriage (Bremmer 1980). In Lesbos, the female poet Sappho wrote about communities of women in which they would learn to love and feel desired (Cantarella 1992). On the pacific islands of Melanesia and Polynesia, transgenerational female-female sexual activity has been documented and was considered a form of sexual play behavior (Deacon 1934). In Tanzania, anthropologists report that adult women participate in demonstrations of sex for young girls, as a rite of passage (Beidelman 1983). Lesotho women practice something called "mummy-baby" relationships between older and younger women in which sexual intimacy and emotional support are central (Gay 1986). Modern examples of female-female transgenerational sex are rare (Greenberg 1988).

Transgendered Female Same-Sex Sexual Expression

Surviving literature from ancient Rome suggests the existence of transgendered sexual relationships between females, with masculine females known as *tribas* preferring a penetrative role in sex with women (Hallett 1989). Several works of fiction describe women who become men, and the Roman natural scientist, Pliny the Elder, described being aware of four such instances of female-to-male transgenderism in the empire (Hallett 1989). Ancient Chinese works of history and literature describe masculine females who entered into long-term group relationships called sisterhoods, enjoyed concubine relationships with high-status wives, and took on male-typical education, occupations, and codes of conduct (Sankar 1986). The *hwame* of the Mohave fulfilled male-typical roles but were considered a third gender and their marriage to women was viewed as normative (Blackwood 1984). Transgendered female-female sexual relationships remain cross-culturally common. In Nigeria and Kenya, women may take on the role of a husband and a father for a female partner with children (Morgan and Wieringa 2005). The Samoan *fa'atama*, the Tongan *fakatangata*, the Hawaiian *mahu*, the Indonesian *cowok*, and the Philippine *lakin-on* each represent highly masculinized female expressions that are culturally sanctioned as a third gender (Besnier 1993; Blackwood 1995; Hart 1968; Robertson 1989). These individuals practice male-typical lifestyles, often marry women, and, in some cases, are regarded as men in their community.

In the West and elsewhere, female homosexuality is frequently expressed in a bipolar masculine/feminine (or "butch" and "femme") pattern (Tripp 1975). The American butch/femme phenomenon has been documented since the first half of the twentieth century (Faderman 1991). Self-identified butch women fulfill male-typical gender norms and are more sexually proceptive (pursuing sexual relationships) than the femme women they tend to pursue. Self-identified femmes fulfill the female-typical gender norms, are generally attracted to masculine traits (Hiestand and Levitt 2005), but prefer the sexual experience provided by self-identified butches, likely including shared female-typical relationship preferences (Bailey et al. 1997; Buss and Schmitt 1993). When asked to place themselves on a continuous measure of butch and femme, 26% of homosexual American women describe themselves as equally butch and femme, and between one and two thirds of homosexual women identify themselves using the terms butch or femme (Levitt and Horne 2002; Loulan 1990; Weber 1996). Butch and femme women have different sexual preferences, with 40% of butch women reporting greatest attraction to femmes and 24% reporting greatest attraction to other butches, whereas 45% of femmes are most attracted to butches and 35% are most attracted to other femmes (the remainders reported no preference). Some lesbian and feminist perspectives have expressed skepticism over the commitment of femmes to the lesbian lifestyle, suggesting that butches are true or "primary" lesbians, whereas femmes are "elective" lesbians or bisexuals (Ponse 1978; Vance and Green 1984). Bisexual women perceive greater stigmatization from homosexual women than from heterosexual women and

are more likely to experience depression and feel disconnected from their community than homosexual women (Baeber 2008; Balsam and Mohr 2007). Future research might explore how public perception of female sexual orientation may influence female sexual expression and the development of female sexual orientation.

Egalitarian Female Same-Sex Sexual Expression

Contemporary Western female-female sexual relationships are commonly egalitarian. In feminist and psychological literature, debate continues as to whether the butch/femme dichotomy has been overstated, exaggerated by twentieth century heteronormative expectations, or socially constructed (Nguyen 2008; Rosario et al. 2009; Walker et al. 2012). However, biological evidence suggests underlying differences between women who identify as butch and femme (see next section). Depending on how restrictively one defines egalitarian female-female sexual relationships, clear examples can be difficult to identify in antiquity. Many of the above examples of transgendered and transgenerational female same-sex sexual expression often cross into egalitarian terrain, where gendered behavior is not clearly divergent and where age differences are minor (e.g., Cantarella 1992; Deacon 1934). This is not to suggest that egalitarian female same-sex relationships are novel; it is more likely that all things female and all things deemed sexually deviant have failed to be recorded by predominantly male historians in predominantly puritanical societies since the rise of scholarship (Studd and Schwenkhagen 2009).

The Biology of Human Female Sexual Orientation

A heritable, biological contribution to sexual orientation has long been hypothesized (e.g., Krafft-Ebing 1922). Heritability (h^2) refers to the proportion of phenotypic variance in a given sample that is statistically attributable to genetic variance in that sample. In other words, heritability indicates to what degree the differences between individuals on a given trait can be explained by differences in their genes, usually measured by their relatedness to one another (Vitzthum 2003). The remaining variance is then explained by intervening environmental forces, which are assumed not to be a function of genetic relatedness. Twin studies provide heritability estimates of sexual orientation between $h^2 = .2$ and .7 for women, and $h^2 = .3$ and .6 for men (Alanko et al. 2010; Bailey et al. 1993; Långström et al. 2010; Pillard and Bailey 1998; Pillard and Weinrich 1986). These are moderate to large estimates for psychological variables; personality variables cluster around $h^2 = .5$ and intelligence between $h^2 = .5$ and .8 (Nisbett et al. 2012). Although genetic markers have not been identified for female sexual orientation, several candidates have been proposed (Burri et al. 2015; Pattatucci and Hamer 1995). If there is a causal pathway from female genetics to sexual orientation, it is likely to involve many genetic loci and it is likely to operate indirectly. For example, gene activity may play a role in hormone production and/or sensitivity, which may subtly influence brain development, which may produce perceptual and behavioral patterns that interact with human social expectations in a way that, in specific circumstances, promotes female-female sexual relationships.

Early research on prenatal hormones and sexual orientation showed no evidence for differences in prenatal hormone levels between homosexual and heterosexual women (Meyer-Bahlburg 1979). Later research found positive correlations between exposure to prenatal androgens (testosterone) and masculine behavior, interest in visual sexual imagery, career orientation, and the likelihood of homosexual and bisexual identification (Money and Ehrhardt 1972; Schwartz and Money 1983). Prenatal androgen exposure has since been linked with male-typical play behavior, reduced satisfaction with female sex assignment, reduced opposite-sex sexual interest, increased same-sex sexual attraction, and increased same-sex sexual behavior (Hines et al. 2004; Money et al. 1984; Reinisch et al. 2017). The results are more pronounced among self-identified butch women, who show higher circulating testosterone levels, more male-typical behavior in childhood, and narrower hips than do femmes (Pearcey et al. 1996; Perkins 1981; Singh et al. 1999). In general, the organizational and activational effects of sex hormones are now considered more powerful than the sex chromosomes in predicting sexual physiology and sexual behavior (Arnold 2009).

Two signals of prenatal androgen exposure have been linked with homosexuality in women: Otoacoustic emissions and finger length ratios. Otoacoustic emissions are small sounds produced by the inner ear due to the acoustic properties of the cochlea. On average, these sounds are more frequent and higher in volume in women than in men (prenatal androgens appear to weaken them), but homosexual women tend to produce less frequent and quieter emissions than heterosexual women, approaching the male pattern (McFadden and Pasanen 1998, 1999). The ratio of index finger length to ring finger length (2D:4D) is lower on average for men and higher for women, such that men tend to have longer ring fingers. Several studies have found that 2D:4D is lower for homosexual women than heterosexual women (and even lower for self-identified butch women; Brown et al. 2002; McFadden and Schubel 2002; Rahman 2005; Rahman and Wilson 2003; Williams et al. 2000). Illustrating prenatal sex-hormone transfer, women who have male fraternal twins also have lower 2D:4D than women who have female fraternal twins (Voracek and Dressler 2007). A meta-analysis comprising 1707 female participants from 16 samples found that homosexual women have a lower average 2D:4D than

heterosexual women, with an effect size of $g = .29$ (Grimbos et al. 2010). Two studies have assessed 2D:4D in monozygotic female twin pairs in which one twin is homosexual and the other is heterosexual, and both found that the homosexual twins had lower, more masculine 2D:4D (Hall and Love 2003; Hiraishi et al. 2012). Above average prenatal exposure to androgens masculinizes female 2D:4D and otoacoustic emissions, and may also masculinize sex-differentiated brain structures, including regions of the hypothalamus and thalamus responsible for sexual attraction and arousal (Levay 1991; Poeppl et al. 2016).

Much can be said about structural brain differences between homosexual men and heterosexual men (e.g., Allen and Gorski 1992; Scamvougeras et al. 1994; Swaab and Hofmann 1990), but few studies have directly assessed brain structure as it relates to human female sexual orientation. A study of 20 homosexual women found that they possessed the male-typical rightward bias in hemispheric volume and functional connections to the amygdala, whereas heterosexual women showed no difference in hemispheric volumes and a leftward bias in amygdala connections (Savic and Lindstrom 2008). Another study of 15 homosexual women found that, relative to heterosexual women, homosexual women possessed significantly lower gray matter concentration in the perirhinal cortex, a sexually dimorphic region which may play a role in object identification, spatial and olfactory processing, and memory (Ponseti et al. 2007). These studies represent early support for the hypothesis that sex-differentiated brain structures show the male-typical pattern in homosexual women.

Female Same-Sex Sexual Behavior in Non-Human Apes

The following coverage of female same-sex sexual behaviors in apes is provided to contextualize human female sexual *behavior*, but does not imply that human sexual expression, with its personal and cultural significance, is deeply analogous to non-human models (for further reading, see Bagemihl 1999; Bailey and Zuk 2009; Poiani 2010; Sommer and Vasey 2006). In nearly every species in which same-sex sexual behaviors are observed, individuals that engage in same-sex sexual behaviors also engage in opposite-sex sexual behaviors (Sommer and Vasey 2006). To the extent that lifetime sexual behavior can be observed or inferred, only a handful of species have individuals that exclusively engage in same-sex sexual behaviors, and all of these individuals are males (e.g., black swans, *Cygnus atratus*, and domesticated sheep, *Ovis aries*; Bagemihl 1999). Across all species, male same-sex sexual behavior is observed more frequently than is female same-sex sexual behavior, although research biases may have motivated greater attention to male sexual behavior. Across primate species, social complexity is positively associated with observations of same-sex sexual behavior (Fernandes et al. 2015). Across bird species, the sex that provides less parental investment engages in more frequent same-sex courtship and sexual behavior (MacFarlane et al. 2010). Across insect species, same-sex sexual behaviors are more common in high density, laboratory conditions, and are largely explained by mistaken identity (discussed below) and pheromone transfer (Scharf and Martin 2013). High sociality, reproductive effort, and same-sex proximity likely reduce the costs associated with same-sex sexual behavior, increasing its frequency, but this does not rule out evolved functions for same-sex sexual behavior. The evolutionary puzzle of same-sex sexual behavior focuses on the costs of sexual behavior (time, energy, and pathogen exposure) when the benefit of reproduction is absent. Hypotheses for the evolution or persistence of female same-sex sexual behavior (reviewed below) thus posit additional, non-reproductive benefits of sexual behavior, propose constraints on the precision of sexual behavior, or dispute the costs of sexual behavior between females.

Orangutans

The Sumatran orangutan (*Pongo pygmaeus*) is commonly described as solitary because they tend to travel, forage, and sleep alone. However, their home ranges overlap, social bands form when fruit is abundant, and sexual consortships can last months with a male and female traveling and copulating before going their separate ways. Female orangutans stimulate and penetrate one another's genitals with their fingers, often while masturbating themselves with a foot (mounting is rare). Females can also develop prolonged same-sex consortships with a favored sexual partner, although these consortships do not appear to involve co-parenting (Galdikas 1995; MacKinnon 1974). In most primates, peak female fertility (estrus) is advertised with conspicuous scents, sexual behavior, and/or bodily signals such as swollen tissues and flushed coloration, and males use these signals to coordinate mating attempts. However, humans and orangutans lack such conspicuous fertility signals and are sexually receptive across the ovulatory cycle (Burley 1979; Knott 2015). This facilitates female mate choice and paternal investment by allowing females to copulate with non-preferred, coercive males during low fertility (encouraging their investment in putative offspring) and to copulate with preferred males during high fertility (increasing the likely genetic quality of offspring; Knott et al. 2010). In the context of female same-sex sexual behavior, continuous sexual receptivity and prudent mate choice may facilitate female-female sexual interactions, if only because females are continuously arousable and preferred males are perceived to be absent or inaccessible (further discussed below).

Gorillas

Gorillas (*Gorilla gorilla*) reside in small polygynous groups consisting of a single dominant male and several adult females who enter the group after dispersing from natal territories. Within the polygynous group, females form pair-bonds with one another and engage in frequent mutual grooming and sexual stimulation, including face-to-face genital rubbing. Researchers describe female-female sexual encounters as more affectionate and lasting five times longer than male-female mountings. Females develop preferred female partners with whom they spend the majority of their time, although these relationships do not appear to involve co-parenting (Fischer and Nadler 1978; Fossey 1983). A recent hypothesis, discussed below, posits that human female-female sexual receptivity is a consequence of a largely polygynous human evolutionary history.

Chimpanzees

Chimpanzees (*Pan troglodytes*) live in mixed-sex groups that contain about twice the number of females as males and can fracture into smaller subgroups or coalesce into large communities. Dispersal is usually female-biased, and mating is promiscuous, with both sexes having multiple opposite-sex partners, and males not contributing significantly to parental care. Females engage in a number of same-sex sexual acts, including rubbing their rumps together, face-to-face genital rubbing, mounting, and genital licking. Female-female pair-bonds are weak and peripheral compared to male-male sexual coalitions, which dominate chimpanzee social and mating structures, and do not produce co-parenting relationships (de Waal 1982; Goodall 1986; Nishida 1997). While in estrus, females will mate with several males per day, and male violence, interference, and rape are common threats to female mate choice. Despite this chaotic and male-dominated mating system, female chimpanzees appear to exert mate choice in a fashion similar to orangutans, with shifting sexual receptivity to preferred versus non-preferred males across the fertility cycle (Stumpf and Boesch 2005). Our closest genetic relatives (particularly bonobos, described below) are among the most sexually active mammals, with a high proportion of nonconceptive sex and a bisexual mating pattern linked to intrasexual alliances that may function to promote mate choice (Wrangham 1993).

Bonobos

Bonobos (*Pan paniscus*) reside in mixed-sex groups that can divide into subgroups and reform, shifting memberships and hierarchies. As in chimpanzees, mating is promiscuous and paternal care is negligible. An important difference between chimpanzee and bonobo society is the presence of a robust network of female-female pair-bonds in bonobos, producing female coalitions that dominate bonobo society and facilitate female mate choice via cooperative defense against coercive males. Frequent female-female sexual interactions appear to maintain these coalitions, and sex may serve as a form of currency (Hohmann and Fruth 2000). Female-female courtship behaviors and a negotiation of sex roles usually precede sexual activity, which is most common between females of differing ranks. Chief among female same-sex behaviors is an intense form of face-to-face genital rubbing wherein a female will lift a clasped partner off of the ground and rhythmically swing them at about two thrusts per second while gazing directly into their eyes until an apparent orgasm is reached. There is speculation that female genital morphology is specifically designed to facilitate this behavior, which occurs once every 2 h for an average female, in equal frequency to heterosexual interactions. Female same-sex behavior supports female-female pair-bonds, which can promote tolerance of the offspring of other females, but female alloparental investment is limited (Blount 1990; Enomoto 1990; Parish 1996). A hypothesis described below places alloparental care at the center of the explanation for human female same-sex sexual behavior.

Evolutionary Hypotheses of Female Same-Sex Sexual Attraction and Behavior

Same-sex sexual attractions and behaviors are puzzling for evolutionary scientists because they exact the costs of sexual activity without a self-evident benefit to survival or reproduction. The list of species that engage in same-sex sexual behavior grows almost as quickly as the necessary observations are made, posing a challenge to the "deleterious anomaly" account of same-sex sexual behavior. Self-identified female homosexuality in humans is associated with about a 20–30% probability of producing at least one offspring, compared to an 80–90% probability of motherhood in the general female population (Gates 2013; Halle 2002; Morris et al. 2002). Because human homosexuality is informed, in part, by genetic factors, one could expect that if these rates persisted across thousands of generations, the relevant genes would diminish in frequency until extreme rarity. However, modern reproductive outcomes do not necessarily reflect average reproductive outcomes across preceding generations (e.g., Symons 1990), and a minority of women who experience same-sex attractions and behaviors identify as homosexual. Biological evolution operates on population-wide differences in average reproductive success across generational time-scales, to the extent that they inform gene frequencies (Darwin 1859). The following accounts of variation in female sexual orientation thus rely on a theoretical history of ancestral human sociosexual environments and the theoretical reproductive consequences of

heritable psychological traits in those environments (Bailey and Zuk 2009). Empirical tests of these hypotheses provide circumstantial evidence for or against the proposed ancestral environments and the proposed reproductive consequences of the traits in question (i.e., human prehistory cannot be observed). This reliance on testing "models" of reality is an intrinsic limitation of the scientific method and need not offend empiricists (Conway and Schaller 2002).

Byproduct Hypotheses

Byproducts are non-functional products of natural selection and adaptations are functional products of natural selection (e.g., Puts and Dawood 2006). The following byproduct hypotheses do not posit direct reproductive benefits for ancestral women who expressed same-sex sexual attraction and behavior. Rather, these hypotheses posit that female same-sex sexual attraction and behavior are a secondary result of events in human evolution and do not themselves solve adaptive problems.

Abnormality and Dysfunction Various hypotheses describe homosexuality as the result of dysfunction, such as hormonal or genetic disorders, developmental instability, social irregularity, or even a pathogen (Bem 1996, 2000; Cochran et al. 2000; Mustanski et al. 2002). Hormonal differentiation of the brain in the prenatal environment was among the first hypothesized sites of dysfunction (Ellis and Ames 1987). Congenital adrenal hyperplasia (CAH) is a genetic disorder that causes the adrenal glands to produce androgens that masculinize the female fetus (Zucker 1999). Diethylstilbestrol was used in the 1950s to treat at-risk pregnancies and had a similar, but less severe, masculinizing effect on female fetuses. Women born under either condition report above average same-sex sexual fantasy and behavior as adults (Meyer-Bahlburg et al. 1995; Meyer-Bahlburg et al. 2008; Money et al. 1984). However, the vast majority of female homosexuals are not the result of identifiable disorders or pharmacology.

The exotic becomes erotic hypothesis (Bem 1996) hinges on the finding that childhood gender-atypical behavior is a strong predictor of adult sexual orientation (Bailey and Zucker 1995). Bem (1996) hypothesized that a heterosexual orientation is calibrated in childhood by associating strongly with members of one's own sex through shared interests and play-styles, while remaining dissociated from peers of the opposite sex. Because most girls find themselves fitting into female social spheres, they come to regard males as outgroup members, and, thus, the more exotic sex. During puberty, the perception of the opposite sex as exotic is translated into the experience of sexual desire in heterosexual women. Thus, female homosexuality begins with a girl's genetic and/or prenatal predisposition for male-typical temperament and interests in childhood, leading to the eroticization of the female social outgroup from which they excluded themselves. This hypothesis is supported by the results of analyses indicating that childhood gender-atypical behavior mediates the association between the shared genetics of twins and their adult sexual orientations (Bem 2000). Critics highlight Bem's selective interpretation of psychological and anthropological data, insensitivity to relevant sex differences, and the fact that an explanation for gender-atypical childhood development is still required (Peplau et al. 1998).

Balancing, Sexually Antagonistic, and Weak Selection The following hypotheses utilize principles from population genetics that can be generally applied to explain the persistence of deleterious heritable traits. The overdominance or heterosis hypothesis describes how a deleterious trait caused by homozygous-recessive alleles can be maintained in the population because, when these alleles are expressed in the more common heterozygotic form, they confer selective advantages. In this case, female sexual orientation may be influenced by genes that can improve reproductive success in the heterozygotic form, but produce exclusive homosexuality in the homozygous form (Gavrilets and Rice 2006; Zietsch et al. 2008). This form of balancing selection maintains deleterious allele combinations in the gene pool as a byproduct of the reproductive benefits of the heterozygote. Exclusively homosexual women could represent the tail-end of a distribution experiencing selection for a linked set of traits that produce more male-typical perception and behavior. In theory, only a small heterozygote advantage is necessary to produce a stable proportion of homozygotes, leading to the persistent, low rate of exclusive homosexuality among women.

The sexual antagonism hypothesis proposes that the genes that contribute to homosexuality in one sex can improve reproductive success when expressed in the opposite sex. In this view, the expression of female homosexuality could be a costly byproduct of selection for genes that produce reproductive adaptations in men. This hypothesis has been proposed only as an explanation for male homosexuality and was inspired by the finding that the female relatives of homosexual men display greater fecundity than the female relatives of heterosexual men, particularly in the maternal line (Camperio-Ciani et al. 2004). Subsequent findings have cast some doubt, producing equivocal results in different samples (King et al. 2005; Rahman et al. 2008; Schwartz et al. 2010), but the hypothesis remains tenable. No genetic loci have been reliably associated with female homosexuality, much less causally linked with female homosexuality. Although the development of these hypotheses center on male homosexuality, for which there exists tentative gene associations (e.g., Hamer et al. 2010), balancing and sexually antagonistic selection remain feasible candidates for explaining female homosexuality, at least in principle.

Rice et al. (2012) provide an additional layer to the sexual antagonism hypothesis for the expression of homosexuality via the transmission of sexually antagonistic epigenetic "epi-marks" from opposite-sex parents to their offspring. Epi-marks are alterations to the structure of the DNA molecule made during the lifespan that are not represented in the nucleotide code (and thus invisible to ordinary genetic assays) but still influence phenotypic expression (e.g., DNA methylation influencing transcription rates). The proposed epi-marks could yield a selective advantage when expressed in a father (e.g., canalized masculinization), become imprinted in the father's germ-line cells (gametes), avoid being erased during early embryonic development, and strengthen androgen signaling pathways in XY fetuses, leading to the targeted masculinization of sexually dimorphic brain-regions in female offspring (Rice et al. 2012). The authors contend that the prevalence of homosexuality, its targeted expression in the brain, its strong familial association, and its low rate of monozygotic twin concordance recommend it as an epigenetically carried trait. The authors also provide calculations demonstrating that, although most epi-marks are erased between generations, a non-negligible proportion survive, and paternal germ-line epi-marks can persist even when the cost to the daughter is greater than the benefit to the father. This exciting hypothesis requires further research, as much of the supporting literature relies on rodent and primate models.

Diamond (2007) points to the independence between arousability and proceptivity (i.e., the motivation to initiate sex) in apes that lack conspicuous ovulation. If arousability is decoupled from proceptivity and continuous throughout the ovulatory cycle, there is little evolutionary reason for women to discriminate between sexual stimuli of different sexes (i.e., becoming aroused by women and engaging in sex with women may not inflict costs on reproductive success). As long as the more sexually proceptive men of the ancestral environment pursued women and sought to arouse them, women who were even predominantly aroused by women could still be reproductively successful. Diamond argues that female sexual fluidity (and, by extension, much of female homosexuality) is due to the absence of selection pressures to curtail female arousability in Homo lineages (Diamond 2007). More recently, Apostolou (2016) put a fine point on this conception of female homosexuality with the weak selection pressures hypothesis. The severity of the costs or benefits produced by a given trait determines the variance of expression in that trait (such that extremely deleterious or advantageous traits more rapidly approach fixation; Keller and Miller 2006). Female same-sex sexual attraction may have had such a minor impact on reproductive success across human evolutionary history that its current expression is the tail-end of the widely distributed traits underlying female sexual orientation. This hypothesis can be challenged on the grounds that it makes tenuous assumptions about ancestral environments. In particular, the possibility that ancestral women had equivalent average reproductive success regardless of their sexual attractions is difficult to imagine or test.

Self-Domestication Self-domestication begins with strong selection for reductions in aggression and results in broad pleiotropic effects across the genome (Hare et al. 2012). Long-term breeding experiments on silver foxes famously demonstrated that selection for the singular ability to tolerate the presence of humans across generations results in neotenization, or delayed maturation, reduced features, prolongation of estrus, and stronger affiliations (Belyaev 1979). The reason for this effect is thought to stem from the fact that these traits arise from a shared genetic locus, whereby selection promoting the genes that underlie "tameness" likewise promote linked developmental traits. Human self-domestication may stem from the benefits gained from social tolerance, cooperation, and linguistic abilities. Individuals who were more socially tolerant, on average, may have secured survival and reproductive advantages as human groups grew and group members became codependent (attenuated by the costs of exploitation). The Homo lineage, in general, is marked by social tolerance, interdependent culture, reduced features, delayed reproduction, and continuous sexual receptivity (compared to Pan, Pongo, and Gorilla lineages). Adult same-sex sexual play is proposed to be one among the suite of traits that are promoted by self-domestication, as juvenile same-sex sexual play is common among primates and may be prolonged into adulthood by the neotenization of the species (Hare et al. 2012). Bonobos, for example, are phenotypically neotenized compared to chimpanzees and adult bonobo same-sex sexual interactions resemble those between juvenile chimpanzees (Palagi 2006). A similar hypothesis suggests that schizophrenia emerged in humans as a result of strong selection on cognition and language faculties (Benítez-Burraco et al. 2017). A moderate rate of human same-sex sexual attractions and behaviors may be maintained as a pleiotropic byproduct of overwhelming selection for social tolerance.

Sexual Frustration and Mistaken Identity Also referred to as heterosexual deprivation, the sexual frustration account of same-sex sexual behavior posits that humans are powerfully motivated to experience sexual and romantic interactions and will pursue them in the absence of viable opposite-sex partners. This hypothesis applies to the real or perceived absence of opposite-sex partners, whether due to demographics (operational sex ratio), environment (all-female institutions), partner preferences ("the men here are not my type"), or low mate-value ("none of the men here are interested in me"). All-female prisons represent the most extreme example, with somewhere between 30 and 60% of female prison inmates engaging in same-sex sexual behaviors and relationships (Owen 1998). Most of these women did not identify as homosexual prior to

incarceration and, the more time women spend in prison, the more accepting they become of sexual interactions between other inmates and of having a "gay cellmate" (Blackburn et al. 2011). Gallup and Suarez (1983) argue that sexual frustration brought on by contradictory human sexual strategies contributes to homosexuality. In other words, what constitutes a "viable" sexual partner may exclude men because they reliably disagree on factors such as the timing and frequency of sex and the expression of emotional and resource commitment. Heterosexual men and women report that sexual relationships inflict greater costs than are reported by homosexual men and women (Duffy and Rusbult 1986). Meanwhile, homosexual men enjoy more rapid and frequent sexual experiences than heterosexual men (on average; Bell and Weinberg 1978; Laumann et al. 1994) and homosexual women report greater sexual satisfaction, more sexual desire, more frequent orgasms, and greater satisfaction with their own bodies than heterosexual women (Coleman et al. 1983; Holmberg and Blair 2009; Morrison et al. 2004; Peplau et al. 1978). Gallup and Suarez (1983) argue that the expression of homosexuality depends primarily on individual differences in the extent and tolerance of heterosexual frustration, along with other social and psychological constraints.

Reliably identifying the sex of a conspecific may seem trivially easy, but apparent misidentification is a source of same-sex sexual behavior in several non-human species (e.g., Bailey and French 2012; Macchiano et al. 2018). Sex identification systems are tasked with avoiding type 1 (incorrectly perceiving a same-sex conspecific to be a member of the opposite sex) and type 2 errors (failing to perceive an opposite-sex conspecific to be a member of the opposite sex), meaning that increasingly conservative criteria for identifying the opposite sex can exclude true members of the opposite sex. In many cases, it is more deleterious to underperceive viable reproductive partners than it is to overperceive them (especially for males). However, the notion of "mistaking" sex identity is a necessary oversimplification when modeling animal behavior and has little utility in human sexuality, but it is worth highlighting here, if only to unpack. An observed "mistake" can have at least two interpretations: Androphilic (male-attracted) women perceive and are attracted to salient male-typical features in biological women and unconsciously "mistake" women for reproductive partners (or consciously mistake them for men, in the rare case), or gynephilic (female-attracted) women have perceptual mechanisms that "mistakenly" tag female-typical features as sexually attractive. In both cases, more nuanced terminology and theoretical considerations can be brought to bear.

Adaptation Theories

To suggest that female same-sex sexual attraction and behavior are the result of adaptation is to suggest that they recurrently served functional roles in survival or reproduction across ancestral human environments. This is not to say, however, that the details of human female sexual expression have remained unchanged over that period, or that the relevant traits contribute to survival and reproduction in modern environments.

Mate Attraction and Male Choice Early evolutionary scholars speculated that female same-sex sexual behaviors served to attract the sexual attention of preferred males or otherwise directly promote female mating success (Kirsch and Rodman 1982). Heterosexual men typically find female-female sexual stimuli highly arousing and a large proportion of male-consumed internet pornography contains female-female sexual interactions (Sakheim et al. 1985; Sun et al. 2010). This suggests that men are attracted to female same-sex sexual behaviors, but no evidence exists to support the notion that women strategically employ these behaviors as a mate attraction tactic. There are at least two sources of data to suggest that bisexually active women produce more offspring than exclusively heterosexual women (at least prior to the age of 25 years; Baker and Bellis 1995; Kanazawa 2016). However, there are also data to the contrary (Essock-Vitale and McGuire 1985). Alternatively, a stable proportion of ancestral men may have preferred female sexual partners who possessed traditionally male-typical traits such as instrumentality, sensation-seeking, risk-taking, and social dominance, traits that may be genetically and/or hormonally linked to female same-sex sexual attractions (Bailey and Zucker 1995; Lippa 2002). In other words, many of the traits that provide a selective advantage in men may have likewise provided a selective advantage in women and may have been linked to sexual attraction to women. Taken to a logical extreme, this hypothesis could imply a coevolutionary relationship between women with male-typical features and preferences and men with female-typical features and preferences, maintained by frequency-dependent selection for complementary, sex-atypical pairings. This novel hypothesis has several challenges, first among them that there is no evidence of complementarity in sex-atypical or androgynous heterosexual relationships (see Green and Kenrick 1994; Lippa 2007).

Alloparenting A defining feature of human embryonic and fetal development is the altriciality of newborns; that is, humans require long gestational periods to reach a large weight (relative to other mammals), and emerge from the womb neurologically and psychologically immature compared to other mammals (Martin 1990). Human neonates require several years after weaning to reach self-sufficiency, and humans do not reach peak foraging efficiency until 20 to 30 years of life (compared to most mammals, who do so soon after weaning; Schuppli et al. 2012). Consequently, human parental investment continues long after birth and

frequently requires assistance from family and community members. Mothers in hunter-gatherer communities can often expect limited investment from the putative father, assuming that he remains in proximity during the pregnancy. Although paternal investment may improve offspring outcomes, it is usually not essential for offspring survival (Chagnon 1992; Hewlett 1988; Hill and Hurtado 1996; Konner 2005; Marlowe 2005; Sear et al. 2002). Even in those cultures that emphasize paternal investment, women cannot guarantee the fidelity of the father and may have adaptations to compensate for his absence. One adaptation may be to evoke alloparental care from related and unrelated females. For example, maternal grandmothers are a consistent and well-studied source of alloparental care, and it has been hypothesized that the female human lifespan extended beyond menopause to facilitate continued investment (Coall and Hertwig 2010).

Women may experience same-sex sexual attractions and establish sexually bonded relationships with other women in part so that they will be more likely to receive alloparental assistance from those women (Kuhle and Radtke 2013). Kuhle and Radtke (2013) highlight the benefits to child-rearing that can be gained by females who are willing to recruit female sexual partners. As described, female bonobos are strongly bonded via sexual behavior and show some alloparental care (e.g., mothers can leave infants with unrelated females for periods of time, food sharing can benefit unrelated infants; Furuichi 2011; Hrdy 2008). All ape and old world monkey females display strong interest in holding and interacting with related and unrelated infants (Hrdy 1976). This is especially true of younger females, whereas males are typically disinterested in infants (Hrdy 1999). Human female children universally engage in pretend play involving domestic and childcare tasks, often using dolls to simulate infants (Draper 1975; Pellegrini and Smith 1998). Cross-cultural research identifies local females as valuable assets in caring for offspring. Survival rates are higher for children who have older female siblings, and mothers whose firstborn is female have greater reproductive success than mothers who first produce boys (Draper and Hames 2000; Flinn 1989; Sear et al. 2002; Turke 1988). Mothers with girls as "helpers at the nest" spend less time performing domestic work and more time socializing (Bove et al. 2002), and alloparental care from unrelated women (usually other mothers) is likewise common and is associated with improved offspring survival (e.g., Hrdy 1999; Ivey 2000; Meehan 2009).

Hrdy (2007, 2008) has proposed that without significant care from unrelated community members, humans could not have raised such altricial young in ancestral environments. Sexual activity and orgasm may promote the sort of pair-bonding a mother might typically have with a provisioning father (Meston and Buss 2007). Indeed, sex between women may more reliably lead to female orgasm than sex between men and women (in modern samples; Frederick et al. 2018). Positive sexual experiences shared between women may lay the foundation for female-female co-parenting engagements, increasing the rate of survival among offspring who could inherit the genetic factors related to same-sex sexual attractions. Although theoretically and comparatively appealing, evidence for same-sex sexual behavior among women who would benefit most from facultative alloparenting (i.e., new mothers and single mothers) is limited (Kuhle and Radtke 2013). This sort of evidence would indicate design specificity in an adaptation for acquiring alloparental support. Some evidence suggests that women who are abused by men in childhood and who have experienced forced heterosexual contact and rape are more likely to identify as homosexual in the USA (Austin et al. 2008; Balsam et al. 2005; Harrison et al. 2008; Ross and Durkin 2005; Scheer et al. 2002). This may suggest that the threat of pregnancy and/or exposure to low-quality male partners may activate adaptations in women to pursue female-female bonds and secure alloparental assistance. However, alternative explanations for these results are available (e.g., negative associations with men), and more research is required to assess this hypothesis.

Polygyny The primary limitations on the practice of polygyny are the concentration of local resources and an individual's ability to defend those resources (i.e., monopolizability; Emlen and Oring 1977). Human agricultural technology afforded an unprecedented escalation in the number of reproductive partners and offspring that a single individual could support. In a survey of the last millennia, reproductive skew in men is greatest in societies that practice agriculture, wherein a small number of agricultural producers or the leaders who control agricultural resources are able to monopolize reproductive access to women at the expense of rivals (Betzig 2012). Around 10,000 years ago, as human life became more sedentary in several independent regions of the world, including Mesopotamia, the Nile, Indus, the Yellow River Valleys, and the valleys of Mexico and Peru, individuals with surplus agricultural resources could, for the first time, attain extraordinary reproductive success (Betzig 2012). This pattern has persisted around the world in more recent history (Betzig 1992, 1995). Although human mating practices are notably diverse and vary with cultural and ecological factors (Marlowe 2003; Schmitt 2015), only about 7% of human cultures lack any observed expression of polygyny, whereas 70% of cultures are primarily polygynous (Murdock 1967). For 85% of human cultures, polygyny is socially permitted, usually in the form of men taking multiple wives as a function of their relative material wealth (White et al. 1988). Anthropologists hypothesize that the culture of monogamy proliferates even as wealth inequality grows because it reduces the intra-group and intra-familial conflict that can make polygyny unstable (Henrich et al. 2012).

The effect of the agricultural revolution is difficult to quantify in phenotypic terms (i.e., it is unknown the degree to which human sexual psychology could have changed across a 10,000-year period). Although the intrasexual selection pressures represented by reproductive skew likely existed in humans long before the rise of agriculture, the severity of the selection pressures exacted by agriculture is worth recognizing. Karmin et al. (2015) analyzed Y chromosome sequences (paternally inherited) and mitochondrial DNA (maternally inherited) from 110 populations around the world and identified a substantial reduction in the effective male population in the millennia following 10,000 years ago. The authors suggest that this sudden decrease in male genetic diversity was caused by cultural changes including agriculture, mass conquest, and the inheritance of status from father to son. In these contexts, the difference between a poor and wealthy male became perversely large, ending most male lineages, and bottlenecking male diversity. Contrast this with female genetic diversity, which steadily increased as the human population ballooned, suggesting that female reproductive skew was not substantially affected by agriculture and that female sexuality was well adapted to the concentration of resources and, presumably, increased polygyny (Karmin et al. 2015).

Kanazawa (2016) underscores the conflict resolution functions of sexual interactions, proposing that in ancestral polygynous arrangements, women who found reliable ways to diffuse conflict would have been better able to collaborate for their own benefit. Specifically, women who lacked a capacity for sexual fluidity may have been less reproductively successful in recurrently polygynous mating contexts due to conflicts with co-wives. Kanazawa points to male interest in female same-sex sexual behavior, increased female sexual fluidity following marriage, and purported female ovulatory synchronization as consistent with this theory. Ethnographic sources (e.g., Bennion 2012; Evans-Pritchard 1970; Murray 2000) also identify sexual interactions between co-wives in a limited number of polygynous societies. This hypothesis implies that female same-sex sexual attractions are designed for polygynous contexts, but no evidence directly links the expression of female-female sexual attraction and behavior to polygyny or reduced conflict, and female intrasexual competition and the common preference for exclusive mating partnerships would seem at odds with this perspective.

Conclusion

In his classic critique, Symons (1990) distinguished "adaptation" from "adaptiveness," reminding theorists that measures of "adaptiveness," or reproductive success, do not provide evidence of "adaptation." An adaptation is a biological machine that survived in the phenotype of an organism over generational time because it conferred greater average reproductive success than alternative designs over that time. All extant organisms are collections of adaptations, a snapshot of surviving phenotypic machines, as currently constituted. Same-sex sexual attraction in a significant proportion of modern women may be responsible for reduced reproductive success in those women, but this does not constitute evidence against female-female sexual attraction as an adaptation. To investigate adaptation, one must triangulate evidence of shared phylogeny, design specificity, and trait associations, imagining those traits expressed in lineages of women across ancestral human environments, in conflict and cooperation with adjacent humans and ecologies. Scientific progress is often a process of dissecting and discarding a priori assumptions. For example, each of the premises for the apparent puzzle of human homosexuality is vulnerable to falsification. Perhaps ancestral same-sex sexual attractions did not result in reduced reproductive success. Perhaps genetic factors do not play a significant role in the development of female same-sex sexual attractions. The apparent evolutionary puzzle of homosexuality may be dissolved by discoveries such as these.

We encourage researchers to make use of phylogenetic and other comparative analyses to track the factors that contribute to the expression of female same-sex sexual attraction and behavior (as in Fernandes et al. 2015; MacFarlane et al. 2010). Uncovering evidence for or against design specificity will require clear predictions regarding the output of psychological mechanisms in well-controlled studies. Women identify as homosexual and enjoy same-sex sexual interactions for reasons unrelated to reproduction, co-parenting, mate attraction, etc. However, women may, for example, experience greater sexual arousal, attraction, or proceptivity toward other women as a function of resource scarcity, parenting demands, or the quality of local males, while controlling for foreseeable confounds. Additionally, psychological adaptations pull together clusters of complementary traits that serve a shared function. Thus, by looking closely at psychological traits that correspond with female same-sex sexual attractions, while looking past cultural superficialities, researchers might identify a cohesive set of functional psychological mechanisms.

Female same-sex sexual attraction is a universal and ancient feature of human sexuality. Yet, little is known about the genetics, neurology, etiology, and historical variance in its expression. Compared to research on males, research on females began late and continues to receive less attention. Many researchers seem to perceive either that explanations for male and female sexual orientations will be identical or that female sexual attractions are irrelevant to human evolution (Herek et al. 1991; Morin 1977). Neither is true. Future theoretical advances may shift our understanding of human female sexual orientation, but we are confident that the information reviewed here will remain relevant to that understanding.

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